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THE FOOD HABITS AND DESCRIPTION OF *ATRICHOPOGON POLLINIVORUS* SP.N. (DIPTERA: CERATOPOGONIDAE).[1]

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With 3 Text-figures.

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Introduction.

The Ceratopogonidae are a family of biting flies with a wide range of food habits. *Culicoides*, *Leptoconops* and *Lasiohelea* pierce the skin and suck the blood of mammals and birds. Species of several genera in the *Forcipomyia* group pierce the wings of dragonflies, moths, lace-wings, etc. drawing blood from the cavities of the veins, and others attack Phasmidae and the larvae of moths and sawflies. The related genus *Atrichopogon* includes a few species that attack beetles of the families Meloïdae and Oedemeridae. Most of the other genera of the family, e.g., *Ceratopogon*, *Serromyia*, *Palpomyia*, catch in flight insects of about their own size, such as Chironomidae and small mayflies, and suck the body fluids, killing their prey in the process (Edwards, 1923). In all these instances, as in other nematocerous biting flies, only the female pierces the host, vertebrate or insect, and takes a blood meal. The blood meal is known, or presumed, to provide the material for the growth of the oöcytes.

In addition to the blood meal of the female, both sexes (again as in other biting Nematocera) take a sugar meal, usually from the nectaries of flowers. The habit has been demonstrated in a number of known blood-sucking species of *Culicoides* (Downes, *in preparation*) and *Leptoconops* (Noè, 1907). Among the

[1] Contribution No. 3284, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada. The observations on food habits were made while the author was on the staff of the University of Glasgow and the taxonomic work was done while in the employ of the Entomology Division, Ottawa.

insectivorous forms it can rarely be shown conclusively that both sugar- and blood-feeding occur in the one species, because of the scarcity of records and frequent doubts about the accuracy of the identification. Nevertheless, females of *Forocipomyia erucicida* Knab, a species that feeds on caterpillars, have been found on the flowers of *Persea* (Knab, 1914) and those of *Pterobosca paludis* Macfie, a blood-sucker of dragonflies, on *Heracleum* (Edwards, 1938). Both sexes of many other Ceratopogonidae, including a number whose females are probably also insect blood-suckers, can be found at the nectaries of various flowers, sometimes in large numbers. The flower-feeding habit is especially well-developed in the genera *Atrichopogon*, *Forcipomyia*, *Dasyhelea* and *Ceratopogon* (personal observations). The females of certain species, however, although probably feeding at flowers, take no blood meal; the unidentified species of *Forcipomyia* and *Dasyhelea* studied by Gad (1951) fall into this category, as the mouth-parts are reduced and non-functional, and possibly other species of *Dasyhelea* also, as a blood-sucking habit has never been satisfactorily demonstrated in this rather common and easily observed genus. With these exceptions, in which the female must provide for the eggs from resources laid down in the larval stage, the blood-sucking habit and the nectar-feeding habit exist together, performing different functions; they are in no sense alternatives or mutually exclusive. This situation also appears to be common to many other biting flies.

In *Atrichopogon pollinivorus*, the hitherto undescribed species which is the subject of this paper, both sexes feed on nectar; and the females, in addition, take a meal of the pollen-sap of honeysuckle. This is the only demonstrated instance, not only in the Ceratopogoniqae but in all the biting Nematocera, in which the female-specific food providing for the development of the oöcytes is derived from a plant source.

The species is very common in parts of western Scotland, and the flowers of honeysuckle are sometimes darkened by masses of these small black midges. The attractiveness of honeysuckle to *A. pavidus* (Winnertz), a close relative, was remarked on by Edwards (1926), but the significance of the habit remained unknown.

Observations on Food Habits.

Most of the observations were made on 3rd and 5th July, 1952, at the Rossdhu (Loch Lomond) Field Station of the University of Glasgow. Both males and females of *A. pollinivorus* were seen to land from flight on or near the flowerheads of honeysuckle. Many of the midges were crawling around slowly exploring the flowerheads, and at times many others were at rest, motionless, on nearby leaves. In general the males outnumbered the females by about two to one.

Individuals of both sexes often found their way into the long, tubular corollas. Many specimens were removed from the corollas and dissected, and the crop was always found to be more or less distended with a clear fluid, undoubtedly nectar. It is the rule for nectar to be taken into the crop (an oesophageal diverticulum) rather than into the stomach in many Ceratopogonidae and in biting Nematocera in general. The nectar flow on these days was very copious, nearly filling the tubes, and many of the midges had been trapped; but some were seen to make their way out safely, and others, with the same fluid in their crops, were found at rest on nearby leaves.

In June, 1949, two females of *Atrichopogon* sp. were seen on flowers of *Prunus lusitanica*, also at Rossdhu, one with the rostrum apparently plunged into an anther, the other sitting on the stigma. The observation indicates that nectar is not the only material sought at flowers, but it was not interpreted at that time. However, in watching the insects on honeysuckle in mid afternoon on 3rd July, 1952, it was again seen that, in addition to those wandering over the petals and into the corollas, there were others at rest on the anthers and, in smaller numbers, on the stigmas. *These individuals were all females.*

Closer inspection showed that these females chose dehisced anthers—the anthers dehisce down the long axis and the pollen-mass is then well exposed—and were probing with the rostrum at the pollen. The insects were not readily disturbed, so that the flowers could be picked and the process observed in more detail under a microscope. Most of the pollen grains were collapsed and dry ; about a quarter, however, were fresh and spherical. Probing continued until a sound grain was discovered and then the tip of the rostrum was applied to it rather firmly, apparently obtaining a grip on the curved surface. A vigorous pulsation of the membranes beside the clypeus, due to the working of muscles of the mouth-parts, then started. After three seconds or so the pollen grain began to collapse, and in another three seconds the contents had been removed and the sides had folded in, leaving the grain in the collapsed state of those around it. The insect immediately moved on and continued the probing until another sound grain was discovered. A female was observed feeding in this way for more than 30 minutes.

At the same time in the afternoon two days later only a few insects were visiting the anthers, and these were readily disturbed and could not be picked for examination. It was found that all the dehisced anthers were empty of pollen, probably because of the drier weather and the varying activities of other insect visitors. In the evening, however, a group of new anthers dehisced, exposing abundant pollen, all intact and plump. At 21.00–22.00 hr. the flowers were again well populated and as many as seven or eight females were often seen probing at the same newly opened anther. One of them taken for observation was still feeding at 2, 12 and 50 minutes after picking ; she was eventually disturbed, apparently by accident, at 110 minutes. This specimen was more restless than those previously studied ; she spent a shorter time on each pollen grain and then, pushing it downward and backward with the rostrum, moved on probing for another. Four other females were placed on a newly opened anther and were left until the following afternoon. A sample of the pollen then showed 16 intact and 61 empty grains ; evidently the destruction of pollen by this species alone is considerable.

Three of the pollen-sucking females were dissected on the afternoon of 3rd July, and six more on the evening of the 5th. The picture was always the same : the crop was distended (in two instances only partially) with an opaque, viscous, creamy-white material ; the stomach contained traces of what was probably the same substance but was not distended. The ovaries were small and undeveloped ; the oöcytes, as seen in live mounts, contained only the merest trace of opaque yolk and filled no more than half of the minute follicles, i.e., they were about equal in size to the group of nutritive cells above them. The condition of the oöcytes, therefore, was much the same as in females of typical species of *Culicoides*, *Simulium*, *Anopheles*, etc., before they have taken a blood meal.

The opaque white material was not found in females taken from corollas, leaves or empty anthers. It seems clear that it is the pollen-sap and that it is taken only by females and before the growth of the oöcytes has started. It is comparable, therefore, to the blood meal of the females of other Ceratopogonidae. There is, however, one interesting difference; the pollen-sap is taken, initially at least, into the crop, whereas in *Culicoides* and most other biting flies the blood is taken into the stomach.

As already mentioned, some females were also seen on the stigmas. The surface of the stigma is sticky and was often heavily coated with pollen grains. Unfortunately none of these females was critically watched or dissected. But some pollen grains taken from stigmas on which females had been seen were mounted in water and many were found to contain large air bubbles, just as did the sucked-out pollen on the anther. It seems, therefore, that anther-visiting and stigma-visiting have the same significance.

The observation of this unexpected food habit was repeated, under somewhat different circumstances, on 23rd May, 1953, when some specimens were found on flowers of hawthorn—again at Rossdhu. Exactly as before, both males and females collected nectar from the base of the corolla while other females crawled up to the anthers. The latter were again observed, under the microscope, sucking out the contents of the pollen grains. The insects collected on this occasion differ from the series from honeysuckle in a number of ways; a discussion of this form is given in the succeeding taxonomic account.

In many places in western Scotland the flowers of iris are even more conspicuously attractive to *Atrichopogon* than those of honeysuckle. The food habits of these iris-visitors are doubtless similar, but there was no opportunity to make any observations. A collection made some years previously shows, however, that they represent yet a third form, intermediate between the two preceding.

Most of the important life processes of the adults of *Atrichopogon pollinivorus* are centred on the honeysuckle flowers and their immediate surroundings. After alighting from a slow, hovering flight both sexes find their sugar meals in the nectar, and the female her blood meal analogue in the pollen. Then, as described elsewhere (Downes, 1955), mating takes place without a swarming flight at chance encounters as the insects crawl over the flowers and leaves (the loss of the habit of mating in flight appears to be related to the reduction of the antennae of the male, described below). Large numbers of both sexes sometimes rest on nearby leaves; some of these have probably not yet fed, but among the females some had partially developed ovaries and had probably fed a day or two previously on pollen from adjacent flowers. Similarly, the hawthorn form not only obtains both foods from the flowers, but also mates there when the sexes meet. In view of these apparently sedentary habits, it is remarkable that the nectar-feeding habit, which provides an energy-source for the adult, is so conspicuous in this species, as compared with many more active biting flies, e.g., *Culicoides*, *Anopheles*, in which it is seen much less frequently.

Description of *A. pollinivorus* sp. n.

Atrichopogon pollinivorus has been referred to in two recent papers (Gad, 1951; Downes, 1955) as *A. pavidus* (Winnertz). Most of the material for these studies, as for the present one, was obtained from honeysuckle flowers

at Rossdhu. Dr. Gad has informed me that his specimens were submitted to Dr. J. W. S. Macfie, who considered that they belonged to *aethiops* (Goetghebuer), and later to Mr. Paul Freeman, who placed them in *pavidus*, a conclusion that Macfie then accepted. In my account of the mating behaviour I followed this determination with reservations. Further study has convinced me that it is a hitherto undescribed species distinct from *pavidus* of Winnertz, as later recognised and more fully described by Goetghebuer (1920, 1934), Kieffer (1925) and Edwards (1926).

The species as defined below shows a considerable range of variation, the greater part of which is due to the existence of three forms. The specimens from honeysuckle at Rossdhu (with which a few females from honeysuckle at Loch Maree, Wester Ross, seem to agree completely) differ slightly from those from iris at the head of Loch Fyne, Argyllshire, and rather more markedly from those from hawthorn at Rossdhu (less than half a mile from the honeysuckle site). The three forms, however, overlap in certain respects and their taxonomic status is not clear. It is not unlikely that they are three species associated with honeysuckle, iris and hawthorn respectively ; it is possible, however, that they are local populations of a species of sedentary habits (see above) collected on different food plants by mere chance. The small number of collections available does not permit a decision on the matter. The description was made from insects taken on honeysuckle at Rossdhu and the type series is entirely from this collection. The points in which the iris and hawthorn forms differ are then noted, but no names are proposed.

Male and *female* : Predominantly blackish, with paler legs and iridescent wings. Eyes pubescent, almost contiguous. Antenna dark brown ; antennal plume of male, when folded, darker. Mesonotum slightly shining black, with many short black setae ; scutellum (fig. 2, H) with two pairs of long bristles, the outer pair slightly the shorter. Pleura and coxae slightly paler than the notum, legs paler still, brownish, unicolorous. Claws, as shown by Nielsen (1951, fig. 7), with a slender bristle on outer side of the enlarged base and with an apical cleft in both sexes (this character appears to have been overlooked in earlier work ; the claws of the males of *Culicoides* are cleft similarly). Haltere, dirty white to pale brown. Abdomen blackish.

Male : Antenna (Table I ; fig. 1, A) and antennal segments variable in length. Segments 3–10 (2–9 of Goetghebuer, Kieffer and Edwards) about as long as segments 11–15 (segments measured in groups as mounted on slide, i.e., including intersegmental membranes ; but not including the basal stalk of segment 3 enclosed in pedicel) ; extreme proportions of 11 specimens, 3–10 : 11–15 = 31 : 32–28 : 24 mm./100. (The figures used to express the proportion also give the actual lengths of the structures in hundredths of a millimetre ; and similarly below.) Segments 11–15 (measured individually without membranes) averaging 4·0 : 4·4 : 6·2 : 5·5 : 8·3 mm./100, but varying to some entent inde-

TABLE I.—*Antennae and genitalia of males of* Atrichopogon pollinivorus *and related forms.*

Origin.	Number of specimens.	Segments of antennae fused.				Numbers of whorl-setae.		Arch of aedeagus.			Central tapering area of aedeagus.		
		4–7.	4–8.	4–9.	4–10.	Seg. 11.	Seg. 12.	Weak.	Moderate.	Strong.	Broad.	Moderate.	Narrow.
Honeysuckle (Rossdhu)	11	8	3	0	0	3 (0–6)	0 (0–1)*	9	1	0	7	2	1
Iris (Loch Fyne)	11	1	2	6	2	2 (0–5)	0 (0)	5	2	4	8	2	1
Hawthorn (Rossdhu)	6	0	0	1	5	6 (5–7)	3 (2–4)	0	2	4	0	1	5

* There is one abnormal specimen with 6 setae on 11 and 1 on 12. The figures for the 10 remaining specimens are : on 11, 2 (0–4) ; on 12, 0 (0).

pendently though always in the order 11 < 12 < 14 < 13 < 15. The long setae of the antennal plume somewhat shorter and less numerous than in most members of the genus (as represented by three undetermined British and Canadian species and five of the six Danish species figured by Nielsen (1951)), so that when folded the pencil of hairs does not extend beyond the middle of segment 13 at the most, instead of to the base of segment 15.

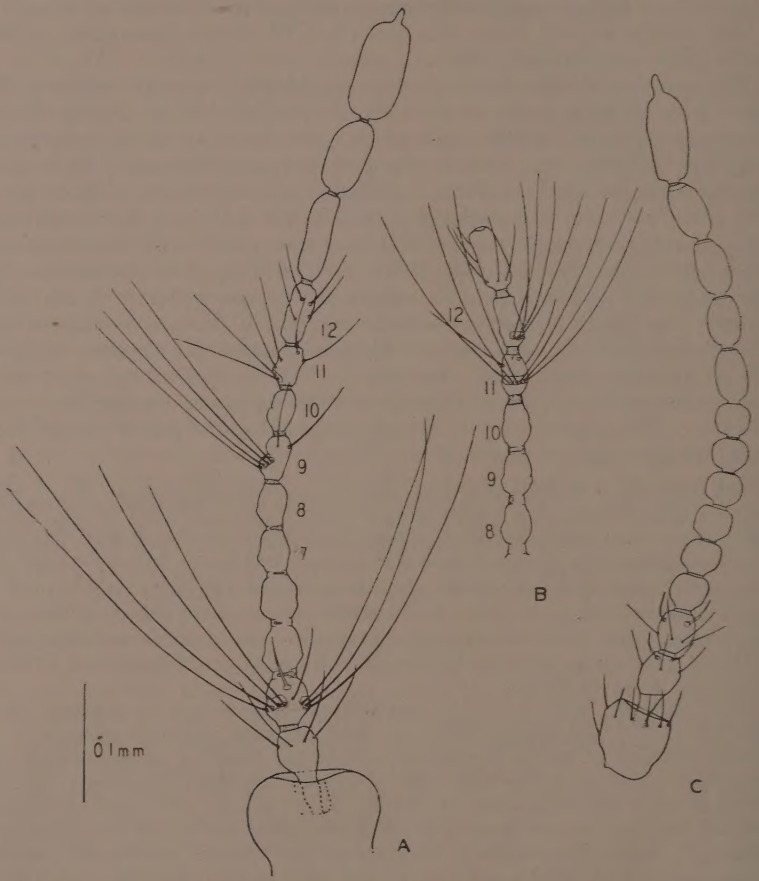

FIG. 1.—Antennae of *Atrichopogon pollinivorus*. A, male of typical (honeysuckle) form; B, male of hawthorn form; C, female of typical form.

On segment 3, as in other species of *Atrichopogon* but unlike *Culicoides*, there are short setae only. Whorls of long setae on segments 4–10, encircling three-quarters (basally) to one-half (apically) of the circumference of the segment, in number about 16 on segment 4 decreasing to about 7 on segment 10; a colourless band enclosing and extending above the basis of the whorls. In the remaining arc one or two short setae somewhat higher up, and still further towards the apex one large and usually one small thin-walled receptor. Toward segment 10, the thin-walled sensilla gradually shifting their positions around the

circumference. On segment 11, the whorl of long setae represented, typically, by two setae only; whorl-setae absent on segment 12 and onwards. The apical segments with numerous short, setiform organs, many probably of the tactile type, others perhaps chemoreceptors. The more basal whorl-bearing segments, segments 4, 5, 6, 7 and sometimes, though imperfectly, 8, joined together by a ring of cuticle of the same colour as the segment

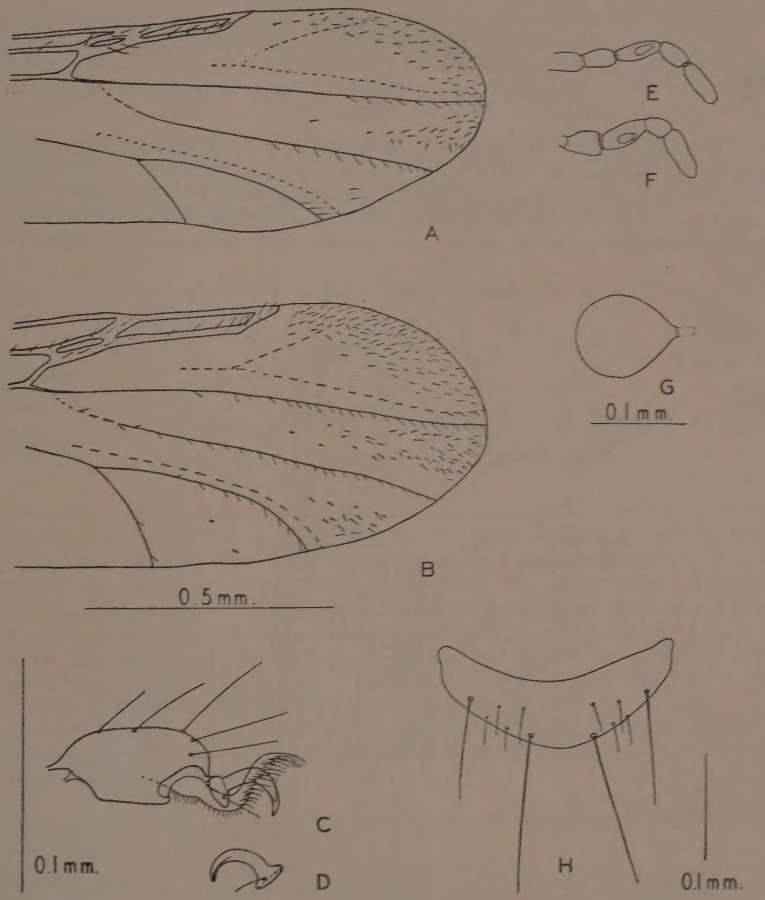

FIG. 2.—*Atrichopogon pollinivorus*, typical form. A, wing of male; B, wing of female; C, last tarsal segment, empodium and claw of female; D, claw of male; E, palp of male; F, palp of female; G, spermatheca; H, scutellum.

itself, usually with a little window of colourless, apparently membranous, cuticle in the ring. Beyond 7 (or 8), the intersegmental regions colourless and membranous.

Palp (fig. 2, E).

Wing (Table II; fig. 2, A): (Tillyard's emendation of the Comstock-Needham system is used; in Edwards' terminology M_{3+4} is the upper branch of the cubital fork.) Length from humeral cross-vein to apex, mean 1·19 mm., range 1·10–1·28 mm.; greatest breadth,

TABLE II.—*Wings of males of* Atrichopogon pollinivorus *and related forms.*

Origin.	Number of specimens.	Setae in cells. M_1	Setae in cells. M_2	Setae on veins. M_2	Setae on veins. M_{3+4}	Ratio of lengths, cell R_2 : cell R_1.
Honeysuckle (Ross-dhu) . . .	11	30 (23–38)	3 (0–9)	13 (8–17)	4 (1–8)	1·6 (1·4–1·8)
Iris (Loch Fyne) .	11	30 (26–38)	2 (0–5)	11 (5–16)	3 (0–4)	1·5 (1·2–1·7)
Hawthorn (Ross-dhu) . . .	6	16 (9–23)	1 (0–2)	4 (0–14)	1 (0–4)	1·6 (1·4–1·8)

mean 0·44 mm., range 0·41–0·46 mm. Cells R_1 and R_2 variable in length, and R_2 ranging from 1·4 to 1·8 times the length of R_1. Cell R_2 ending just short of, or approximately above, the intercalary fork. M_{3+4} and Cu_1 branching below the outer half of cell R_1. Setae on anterior veins and near the apex only; a considerable field in cell R_5, a smaller field in cell M_1 and a few only in M_2; on the veins, fairly numerous on M_2 and a few on M_{3+4}.

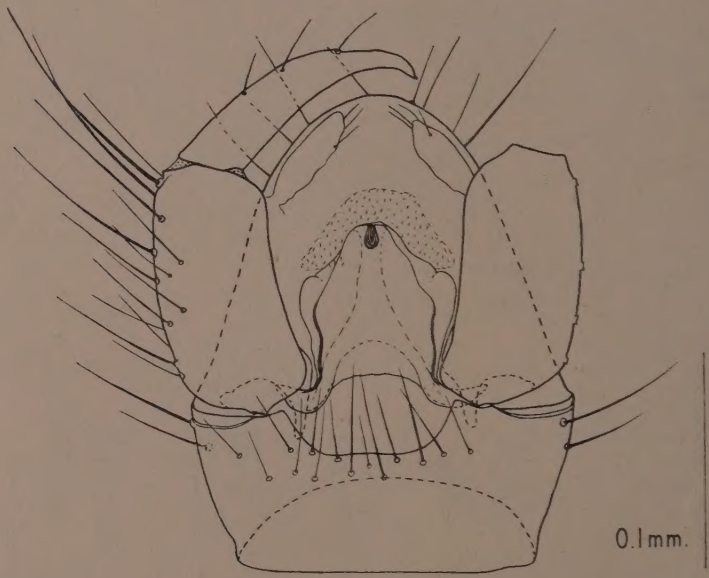

FIG. 3.—Terminalia of *Atrichopogon pollinivorus*, the smaller setae of coxite and cerci omitted; male of hawthorn form.

Legs: Segments of hind legs approximately as follows: femur : tibia : tarsus 1 : t. 2 : t. 3 : t. 4 : t. 5 = 48 : 44 : 19 : 8 : 5·5 : 4 : 5·5 mm./100. Claws (fig. 2, D), as noted, deeply bifid, the two teeth of similar length.

Terminalia (Table I; see also fig. 3, made from a specimen on hawthorn): Tergite elongate, extending well beyond the coxite, somewhat tapering and with a broadly rounded hind margin. Dorsal surface with scattered setae of moderate length, rather denser toward the hind margin; but the elongate furrow, described by Goetghebuer (1920) in *A. pavidus*, apparently absent. Sternite with a large, roughly semicircular emargination,

in front of which are 8–15 setae, more or less in a row. Coxite and clasper as shown; coxite with a single, strong, blunt root, possibly the homologue of the dorsal root of *Culicoides*. Aedeagus generally as in figure, the main shield-shaped area largely rather membranous and supported by a basal arch with limbs strongly sclerotised, but usually somewhat weaker centrally; above the arch a lightly sclerotised, tapering central area, which is usually broader than shown in figure. Parameres, if present, not recognised. Beyond the aedeagus a triangular area with short tooth-like bristles, apparently the anal tube. Cerci with short setae, lying below the sides of the curved margin of the tergite.

Female : Antenna (fig. 1, c) shorter than in male, but again variable. Segments 3–10 averaging one-tenth shorter than 11–15, extremes of six specimens 24 : 28–25 : 26 mm. 100. Segments 11–15 measured individually averaging 4·3 : 4·3 : 4·8 : 5·1 : 8·4 mm. 100, rather constant in length except for segment 15, which ranges from 8·0 to 9·2 mm. 100. Segments 4–10 each with a verticil of 8 setae, and above these 3 large and 1 small thin-walled sensilla. On segment 11 and onwards the verticil setae weaker and many other small setiform organs present. The antennae of the female were not studied in great detail.

Palp (fig. 2, f).

TABLE III.—*Wings of females of* Atrichopogon pollinivorus *and related forms.*

Origin.	Number of specimens.	Setae in cells.			Setae on veins.			Ratio of lengths, cell R_2 : cell R_1.
		M_1	M_2	M_4	M_2	M_{3+4}	Cu_1	
Honeysuckle (Rossdhu)	6	48 (44–58)	18 (12–21)	1 (0–2)	20 (17–23)	10 (8–11)	1 (0–2)	2·5 (2·2–2·7)
Honeysuckle (Loch Maree)	3	44 (40–46)	14 (7–18)	2 (0–4)	20 (20–21)	11 (10–12)	2 (1–5)	2·4 (2·2–2·6)
Iris (Loch Fyne)	3	28 (26–31)	6 (5–7)	0 (0)	17 (13–20)	7 (4–10)	1 (0–4)	2·4 (2·2–2·6)
Hawthorn (Rossdhu)	3	21 (12–30)	2 (1–4)	0 (0)	14 (10–16)	6 (3–8)	0 (0)	3·0 (2·9–3·1)

Wing (Table III; fig. 2, b) : Length, average 1·34 mm., range 1·26–1·40 mm.; breadth average 0·55 mm., range 0·51–0·59 mm. Radial cells again variable, but cell R_2 much longer than in male, from 2·2–2·7 times as long as cell R_1. Cell R_2 ending above or just beyond the intercalary fork. M_{3+4} and Cu_1 branching below the outer half of cell R_1. Macrotrchia again mainly anterior and apical, considerably more numerous than in male in the corresponding fields, and occasional setae also in cell M_4 and on vein Cu_1.

Legs : Segments of hind legs approximately as follows : femur : tibia : tarsus 1 : t. 2 : t. 3 : t. 4 : t. 5 = 52 : 45 : 21 : 8 : 7 : 5 : 7 mm./100. Claws (fig. 2, c) deeply bifid, the outer tooth considerably longer than the inner.

Abdomen : Sterna of all segments normal, i.e., segments 6 and 7 without projecting appendages, segment 8 not emarginate. Spermatheca (fig. 2, g) one, suboval, with short tapering neck, about 110 × 85 μ.

Holotype ♂, and *allotype*, DUNBARTONSHIRE : Rossdhu, 5.vii.1952, on honeysuckle.

Paratypes, 48 ♂, 57 ♀, DUNBARTONSHIRE : Rossdhu, 3 and 5.vii.1952, on honeysuckle.

Other specimens, 8♀, WESTER ROSS : Loch Maree, vii.1952, (*Prof. J. Walton*). These cannot be distinguished in any way from the females of the type series (see Table III).

Specimens on hawthorn.—The significant features of this series are set out in Tables I–III. The form is characterised by a much reduced number of setae in all fields of the wing, so that they disappear entirely in cell M_4 and on vein Cu_1 of the female and are reduced to an average of 1 in cell M_2 and on vein M_{3+4} of the male. The tables show that an absolute separation of the honeysuckle and hawthorn forms could be made on this feature alone. The ratio of the lengths of cell R_2 and cell R_1 is the same as in the honey-

suckle form in the males, but distinctly greater (average 3·0, with no overlapping of ranges) in the females.

The *male terminalia* (fig. 3) differ, but with some overlapping, in that the basal arch of the aedeagus is usually strongly sclerotised centrally and the lightly sclerotised tapering area above it is narrow, as figured.

The *antenna* of the male (fig. 1, B) is also distinctive. The long whorl-setae extend further up the shaft: an almost complete set (for an apical segment) of 5–7 setae occur on segment 11, and there are usually 3 on segment 12. The fusion of the flagellar segments is more extensive, segments 4–10 (usually) being more or less joined together by sclerotised intersegmental regions. Nevertheless, the length and number of the whorl-hairs of this form also are somewhat less than in a typical member of the genus.

Specimens examined, 12 ♂, 3 ♀, DUNBARTONSHIRE: Rossdhu, 23.v.1953, on hawthorn.

Specimens on iris.—The significant features are set out in Tables I–III. The form is intermediate between those on honeysuckle and on hawthorn in a number of ways. As a series it is readily definable, but because of the ranges of variation some individuals cannot be distinguished from the honeysuckle form. The females, only three in number, give intermediate wing-seta counts in all fields, but the radial cells resemble those of the honeysuckle insects. The males, however, have the same number of wing-setae as those on honeysuckle, so that the sexual dimorphism in this feature, shown by the two other forms, does not occur.

In the *male terminalia* the arch of the aedeagus and the tapering area are both variable but closer to those of honeysuckle specimens.

The *antenna* of the male has whorl-setae as much reduced as in honeysuckle specimens, but the fusion of the segments is more variable and, on the average, in an intermediate condition.

Specimens examined, 49 ♂, 3 ♀, ARGYLLSHIRE; head of Loch Fyne, 21.vii.1947, on iris.

A random selection of specimens of each form (numbers given in tables) were mounted on slides for detailed study. All measurements in the text and tables are derived from these specimens alone and only a general comparison of the remainder was made. In all those on slides, detailed measurements were also made on the following features: *Females:* length and breadth of wing, lengths of antennal segments 3—10 and 11–15 and of 11, 12, 13, 14 and 15 individually, shape of spermatheca; *Males:* the same features of wings and antenna, number of hairs on the emargination of sternite 9, and the general features of the terminalia. No differences from the conditions described for the honeysuckle form were detected in any of these features.

The holotype, allotype, a series of paratypes and representatives of the hawthorn and iris forms have been deposited in the British Museum (Natural History). A series of paratypes and other representatives have also been placed in the Canadian National Collection and in the U.S. National Museum.

In all three forms of *A. pollinivorus* the wing of each sex is more hairy than shown in the figures associated with Winnertz' original description of *A. pavidus* (1852, fig. 25). In the typical form, on honeysuckle, in which the difference is greatest, females have a considerable field of setae in cell M_2 and on vein M_{3-4}, with a few beyond, and the males have many on vein M_2 with a few beyond; but none of these areas has any setae in Winnertz' figures. The legs, moreover, are almost unicolorous; the femur and tibia could hardly be described as being

darkened at the apices. The tergite of the male terminalia, alike in all three forms, differs from Goetghebuer's description of *pavidus* (1920 : 35 and fig. 20) in extending well beyond the coxites and being broadly rounded apically. In the antennae of the male, segments 3–10 and 11–15 are almost equal, as compared with a ratio of 48 : 42 in *pavidus*, but the proportions of segments 11–15 among themselves are very similar in the two forms. In the female, segments 3–10 : 11–15 = 9 : 10 approximately ; the difference is probably greater in *pavidus* (Goetghebuer (1934, p. 26) gives a ratio of 44 : 54 for the lengths of segments 3–9 (probably intending 3–10) to 11–15 ; Kieffer (1925) has 44 : 56 for segments 3–10 : 11–15).

A. pollinivorus differs from *A. aethiops* (Goetghebuer), another closely related species, in the same way as from *pavidus* with regard to the wings. The tergite of the male terminalia of *aethiops* is elongate and rounded apically, as in *pollinivorus*, but is much narrower (Goetghebuer, 1920, fig. 18). In the antenna of the male, segments 3–10 are shorter than 11–15 (40 : 45) rather than equal ; and in the female the ratio is 31 : 40, as compared with 9 : 10 for *pollinivorus*. The haltere of *aethiops* is brownish-black, instead of pale, and the seventh sternite of the female is deeply emarginate, instead of normal as in *pollinivorus*.

The three forms of *pollinivorus* are closer to one another than to *pavidus* or *aethiops* and differ from these two species to the same extent in all the characters mentioned above except that of the distribution of setae on the wings, in which, as already noted, they show differences among themselves.

A. pollinivorus, *pavidus* and *aethiops* seem to form a fairly distinct and natural group within the genus *Atrichopogon*. The eyes of all three are pubescent (subgenus *Kempia*), the sixth sternite of the female is unmodified (thus differing from *hamiferus* (Goetghebuer) and *appendiculatus* (Goetghebuer) among the recognised British species), in the antenna of the female segments 3–10 are only slightly shorter than segments 11–15, and there is no very pronounced sexual dimorphism in the distribution of setae on the wings (in both ways differing from *fuscus* (Meigen) and *brunnipes* (Meigen)). The tergite of the male terminalia is much longer than in *fuscus* or *hamiferus*.

Discussion.

It seems, therefore, that there are at least three pollen-eating forms of *Atrichopogon* in Britain, for all of which, in the present state of knowledge, the name *A. pollinivorus* may be used. Presumably, if Edwards' determination of his honeysuckle insects as *A. pavidus* (Winnertz) is correct, they represent a fourth member of the same food habit group. It is not unlikely that the Oriental species *A. jacobsoni* de Meijere is also a pollen feeder, since Tokunaga (1940 : 186) has shown that it forms resting clusters on the leaves of *Hibiscus*, *Mangifera*, etc., that strongly recall those of *A. pollinivorus* on the leaves around the flower-heads of honeysuckle.

These are the only known instances in any of the blood-sucking families of Nematocera in which the female-specific food is obtained from a plant source. In the Culicidae, however, there are two old observations that could bear the same interpretation, but they remain unconfirmed and their significance is very doubtful. Ficalbi (1890) captured specimens of *Culex phytophagus* Ficalbi with a green material, which, he said, evidently contained chlorophyll, in the

stomach. Edwards (1932), however, placed *phytophagus* in synonymy with *pipiens* L., a species with typical blood-sucking habits. Howard, Dyar and Knab (1912, **1** : 110), in referring to Ficalbi's observation, make it appear more precise and complete than it is in the original text. Secondly, Hatchett Jackson (*in* Theobald, 1903, **3** : 151) reported that he had seen females of *Culiseta annulata* (Schrank) piercing the stems of periwinkle and wallflower and apparently sucking the juices. *C. annulata* is also a well-known bloodsucking species. There is also an observation by Britten (1937) that might easily be confused with these, but which seems to have a different significance. He reported that females of *Culex pipiens* and of *Taeniorhynchus richiardii* (Ficalbi) pierced the bracts of the flower-head of *Cnicus* : but by so doing they obtained nectar from the enclosed florets, not a protein-containing food.

The only female-specific foods recorded hitherto in the genus *Atrichopogon* are beetles of the families Meloïdae and Oedemeridae, the moth *Stauropus* and mealy-bugs. In Europe and North Africa *A. rostratus* and *A. meloëzugans* Kieffer hover around *Meloë* and attack the beetles through the membranous areas of the body (Peyerimhoff, 1917 : Kieffer, 1922 : Hansen, 1921 : Edwards 1923 : Blair, 1937 : Storå, 1939) and in North America several undetermined species feed on *Epicauta* (Farr, 1954). Korschefsky (1937) noticed that *A. rostratus* is attracted to both living and dead *Meloë*, and Gornitz (1937) showed that cantharidin, an extract of meloid beetles, is a highly specific attractant of *A. brunnipes* (Meigen), a species whose natural food is not known. Less well known is the discovery of Krogerus (*in* Storå, 1937) that *A. oedemerarum* Storå is associated with Oedemeridae. These midges were first found attached to museum specimens of *Oedemera flavescens* (L.) and experiments in the field then showed that they were attracted not only to this species but also to *Chrysanthia viridis* Schm. and *C. viridissima* (L.). Vogel (1930) found *A. infuscus* Goetghebuer sucking the wing veins of *Stauropus fagi* (L.) (Lepidoptera), an observation which recalls the similar habits of species of *Forcipomyia*. Edwards (1939 : 25) mentions, without reference, that a species of *Atrichopogon* attacks mealy-bugs in southern India. It is remarkable to find two such different foods as pollen-sap and the blood of insects utilised in the same genus. On the other hand, *A. pollinivorus* is not very closely related to *A. rostratus*, *A. meloëzugans* or *A. oedemerarum*, the first having pubescent eyes (subgenus *Kempia*) and the others bare eyes (subgenus *Atrichopogon*). *A. brunnipes* and *A. infuscus*, however, are species of *Kempia*, though again not close to *pollinivorus*.

I am inclined to believe, in spite of the many records from Meloïdae, that neither the meloid- nor the pollen-eating habit is extensively developed in *Atrichopogon*. The genus is generally common and widespread in Britain and in eastern Ontario and southern Quebec, but in none of these areas are meloids at all abundant. At Churchill, Manitoba, where several species of *Atrichopogon* (representing both subgenera) are abundant, meloids are absent. Since the discovery of the female-specific food of *A. pollinivorus*, many hundreds of *Atrichopogon* have been observed on flowers at Churchill, principally on *Cicuta* and *Heracleum* (Umbelliferae) but also on *Rorippa* (Cruciferae), *Epilobium* and *Ledum*, and similar large numbers on *Spiraea*, *Mentha* and *Chrysanthemum* at Rowanton Depot, Quebec. Without exception these individuals probed at the nectaries, and showed no interest in the anthers or stigmas. Many of the nectar-feeding females at Churchill had a red substance in the stomach, but in

spite of considerable observation and experiment the source of this material was not discovered. The records of species attacking Oedemeridae, moths and mealybugs, which were not known to me at that time, suggest, however, that the majority of the species are insectivorous.

The mouth-parts of *Atrichopogon pollinivorus* have been studied by Gad (1951). He showed that the mandible of the female has strong apical teeth, whereas the labrum and hypopharynx (and the lacinia) are tapering organs devoid of rigid armature, though the labrum bears a rather conspicuous apical group of bristles. In the female of *Culicoides*, which cuts through the skin of vertebrates, and of the several genera that attack other insects, not only the mandible but also the labrum and hypopharynx (and sometimes the lacinia) are armoured and evidently play a part in piercing the integument and entering the wound. In the non-piercing males of all genera and in the females also of a species of *Forcipomyia* that is evidently not a blood-sucker, the mandibles are weak, reduced organs and the labrum and hypopharynx are unarmoured and resemble in a general way those of *A. pollinivorus*.

The mouth-parts of *A. pollinivorus* comprise, therefore, mandibles that resemble the fully functional organs of *Culicoides* and a labrum and hypopharynx much like those of non-piercing forms. This fact caused Gad some difficulty in his attempt to classify the mouth-parts into types related to the various food habits, but it seems readily interpretable now that the food habits of the species are known. The mandibles are evidently the organs used to cut open the pollen grain, while it is being held, most probably, by the bristled tip of the labrum in front and the apex of the labium behind. After the grain has been cut open it is merely sucked out : there is no need, or space, for the fascicle (the whole group of structures that are sheathed by the labium) to enter a wound.

Gad classified the mouth-parts of Ceratopogonidae into three groups and correlated them with vertebrate-piercing, insect-piercing and nectar-feeding food habits. He finally decided to place *Atrichopogon pollinivorus* in the nectar-feeding group because of its well-known flower-visiting habit, thus leaving the fully developed mandibles unexplained. It is clear from what has already been said, however, that nectar-feeding and blood-sucking are not comparable, alternative food habits, but habits of different orders that may occur together in the one species. The correctly placed members of Gad's nectar-feeding group are those species—of *Forcipomyia* and *Dasyhelea*—that are *only* nectar-feeding and that have *lost* the blood-sucking (or analogous) habit, in association, presumably, with the ability of the female to provide for the development of the eggs from internal resources laid down in the larval stage. Their mouth-parts are therefore merely reduced, not specialised for nectar-feeding. *Atrichopogon pollinivorus* should be excluded from this group and a new one should be established to receive it ; both sexes feed on nectar and the females also on pollen-sap, and the female, as Gad's paper shows, has mouth-parts differing from those of other Ceratopogonidae and adapted for obtaining her specific food.

Summary.

1. Both sexes of a new species of *Atrichopogon* feed on the nectar of honeysuckle and the females also pierce the pollen grains and ingest the sap. The feeding habits are described in detail.

2. The meal of pollen-sap is the analogue of the blood-meal of the females of other Ceratopogonidae and of blood-sucking flies generally. It is the only established instance of a " blood-sucking " nematoceron obtaining the female-specific food from a plant source.

3. Females of several other species of *Atrichopogon* feed on the blood of Meloïdae and Oedemeridae (Coleoptera), another has been recorded from the moth *Stauropus* and yet another from mealy-bugs. It does not seem likely that either the meloid- or the pollen-eating habit is widespread in the genus.

4. The mouth-parts are discussed, and Gad's classification of the mouth-parts of the Ceratopogonidae by food-habit types is emended.

5. *Atrichopogon pollinivorus* sp. n. is described and figured. Two closely related forms, possibly distinct species, which are associated with hawthorn and with iris, are also described but not named.

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